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Molecular characterization of the non-costate morphotypes of buliminid foraminifers based on internal transcribed region of ribosomal DNA (ITS rDNA) sequence data

Masashi Tsuchiya *, Masatoshi Tazume, Hiroshi Kitazato

Japan Agency for Marine-Earth Science and Technology, Institute for Research on Earth Evolution, Research Program for Paleoenvironment, 2-15 Natsushima-cho, Yokosuka 237-0061, Japan

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ABSTRACT

We performed molecular phylogenetic analyses of four morphotypes of the benthic foraminiferal genus *Bulimina* (*B. aculeata*, *B. marginata* f. *marginata*, *B. marginata* f. *denudata*, and *B. elongata*) based on sequences of internal transcribed spacer region of ribosomal DNA (ITS rDNA). Six genetically distinct phylotypes were revealed by our phylogenetic analyses. The six phylotypes basically correspond to the fundamental morphotypes: clades A+B (*B. aculeata*); clade C (*B. elongata*); clade D (*B. marginata* f. *denudata*); clade E (*B. marginata* f. *marginata* genotype 1); and clade F (*B. marginata* f. *marginata* genotype 2). All six phylotypes are well distinguished, except phylotype B, which shows only little sequence divergence compared to clade A, possibly indicating that genetic differentiation is in progress. Morphological characters including the direction, placement, and shape of spines, the angle of undercutting of chamber periphery, and the roundness of the chambers were stable among specimens of each clade. In contrast, the length and density of spines, and chamber size, were variable within each clade. These intermediate morphological characters may reflect ecophenotypic variation. Our study clearly shows that the examined *B. acuelata*, *elongata*, and *denudata* morphospecies are genetically separated and that *B. marginata* is a species complex comprising several genotypes. A novel phylotype represent different morphotype compare to *B. marginata* f. *marginata* that can be distinguished based on differences of chamber angularity, the direction, placement, and shape of spines, and test dimensions.

1. Introduction

Foraminifera of the genus *Bulimina* have adapted to various environmental conditions, and each species has a distinct distribution pattern, with members of the genus ranging from sublittoral to bathyal depths (Pflum and Frerichs, 1976; Culvar and Buzas, 1980; Inoue, 1980; Lutze, 1980). Because buliminid species show habitat segregation, such as bathymetrical segregation in relation to various oceanic environments, they are applied as proxies of past and/or recent oceanic environments (e.g., Inoue, 1980; Jorissen, 1988; Hayward et al., 2004; Nomaki et al., 2005, 2006). However, morphology-based taxonomy of buliminids is problematic, because of the occurrence of intermediate morphologies between the non-costate morphotypes among four buliminid species of *B. aculeata*, *B. marginata*, *B. denudata* and *B. elongata*. Intermediate morphologies successively vary between these species groups, elongate types exist especially between *B. denudata* and *B. aculeata* (e.g., Jorissen, 1988; Collins, 1989; Burgess and Schnitker, 1990).

Bulimina aculeata and *B. marginata* were described by d'Orbigny in 1826 from recent sediment samples from the Adriatic Sea. Both species were distinguished by d'Orbigny based on chamber angularity, location and length of spines, and test dimensions. Jorissen (1988) studying Adriatic Sea non-costate buliminid divided *B. marginata* into three morphotypes, which reflected morphological changes related

* Corresponding author. Tel.: +81 46 867 9793; fax: +81 46 867 9775.
E-mail address: tsuchiyam@jamstec.go.jp (M. Tsuchiya).

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to water depth: *B. marginata* f. *denudata* (30–50 m), *B. marginata* f. *marginata* and *B. marginata* f. *aculeata* coexisting without any intermediate morphotypes deeper than 50 m. *Bulimina marginata* f. *marginata* was not found at depths shallower than 50 m. Morphological succession between the three morphotypes was present within the same depth range between 30 and 50 m.

Over the years, however, taxonomists have debated whether these two morphogroups should be discriminated as the species *B. aculeata* and *B. marginata* (e.g., d'Orbigny, 1826; Collins, 1989; Burgess and Schnitker, 1990) or whether they are members of the same polymorphic species (e.g., Hoeglund, 1947).

Both Collins (1989) and Burgess and Schnitker (1990) concluded that *B. aculeata* and *B. marginata* could be considered as distinct species, with an intermediate morphotype representing the morphological variation of *B. marginata*. Burgess and Schnitker (1990) performed morphometric analysis of the *B. marginata* and *B. aculeata* morphogroups from sediment cores in Wilkinson Basin. They discussed the assemblage transition between both species and concluded that their morphological divergence resulted from changes in the bottom water source of North Atlantic slope water, leading to the occasional local formation of colder and less saline water. Smith (1964) reported that the number of spines of *B. marginata* f. *denudata* was related to water depth, loss of spines occurred in relation to water depth increase.

According to Collins (1989), chamber inflation and the number of chambers per length are the main morphological characters that delineate *B. aculeata* and *B. marginata* as two distinct species. With regard to these characters, a morphocline exists between the species, and the morphological variation appeared to be related to the species' interregional distributions. Morphometric analysis based on canonical

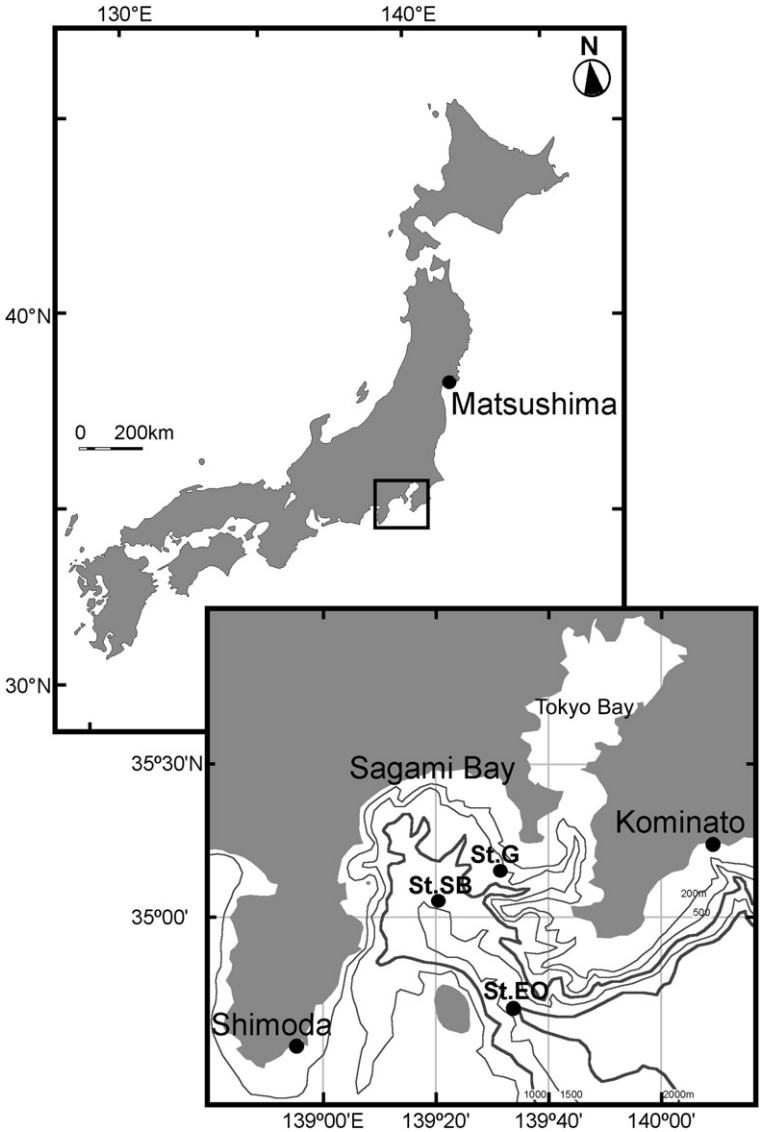

Fig. 1. Sampling localities of buliminids off the Japanese Islands.